# Earthworm and Enchytraeid Co-occurrence Pattern in Organic and Conventional Farming: Consequences for Ecosystem Engineering

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**Abstract:** Earthworms and enchytraeids are ecosystem engineers with an important influence on soil structure maintenance and nutrient cycling. We investigated if different agricultural managements produce a replacement of earthworms by enchytraeids, the magnitude of that replacement, and its effect on ecosystem engineering activities. Organic farming with plough tillage (ORG), conventional farming with plough tillage, conventional farming with no-tillage (NT), and unmanaged natural grasslands were studied. Earthworms and enchytraeids were sampled by means of extracting and hand sorting soil monoliths. Soil bulk density, mechanical resistance, organic matter content, and litter decomposition were measured as indicators of soil structure maintenance and nutrient cycling. A negative relation between earthworm and enchytraeid abundances was confirmed, not related to tillage intensity. Competitive interactions between them are suggested. Among agricultural systems, ORG had the highest earthworm abundance and NT had the highest enchytraeids abundance and the highest enchytraeid-to-earthworm ratio. Besides, intermediate abundances of earthworms and enchytraeids promoted by ORG were related to soil structure indicators' values similar to grassland and enhanced litter decomposition process. Despite a higher abundance of enchytraeids in NT, both soil structure maintenance and nutrient cycling indicators had worse values than those in ORG.

**Key Words:** Earthworms, enchytraeids, no-tillage, organic farming, soil functioning, sustainability

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Earthworms are one of the emblematic components of the ecosystem engineers' functional guild because they are widely distributed worldwide and they have the ability to alter soil, creating specific structures—for example, burrows, galleries, and chambers—as well as casts and fecal pellets resulting from their feeding activities (Lavelle, 1997). Enchytraeids are among the most important components of the soil decomposer community. They are small Oligochaeta (body length from 1 to 50 mm) that live in aquatic and terrestrial environments (Lavelle and Spain, 2003). From the total of 600 species described, 62 species have been cited for South American region (Lavelle and Spain, 2003; Christoffersen, 2010). Their engineering ability has been frequently neglected. However, they can also be referred to as "microengineers" (Didden, 1990; Brussaard et al., 1997) because their significant effects on physical properties have been frequently observed in soils (Lavelle et al., 2006). Although at finer scale compared with earthworms, enchytraeids modify soil structure by means of their movement through the soil that favors aeration and water infiltration. Being soil-ingesting animals, they also influence the younger fraction of organic matter by including components of litter in feces aggregates and mixing them with clay particles (Marinissen and Didden, 1997). Several publications have suggested that earthworm and enchytraeids may be mutually exclusive mainly because enchytraeids seem to be more resistant to the impact of agricultural practices and are weak competitors in soils with high earthworm abundances (Wardle, 1995; Nowak, 2004). Besides, some studies have shown that tillage shifts the relative importance of the Annelida from earthworms to enchytraeids (Nowak, 2004; van Vliet et al., 2004). Although there are studies that have assessed the relationship between earthworms and enchytraeids in no-till versus plough tillage, both conventional farming systems, much less is known about this relationship in organic versus conventional farming.

Indeed, in Argentina, the most used farming system is currently conventional agriculture with high dependence on synthetic agrochemicals, and recently no-till practices have been widely adopted (AAPRESID, 2012). However, for the last 20 years, organic farming has also had an important increase—of about five times in crop and almost 30 times in cattle production (SENASA, 2014). Organic farming attempts to maximize the reliance on farm-derived renewable resources and in the management of ecological and biological processes and interactions so as to provide acceptable levels of crop, livestock and human nutrition, protection from pests and disease, and an appropriate return to human and other resources (Lampkin, 1994). Hence, this production system has been by far the most widespread and adopted worldwide to fulfill the purpose of a sustainable agriculture (Rigby and Cáceres, 2001). A major feature of practicing agriculture in this way is that the reduced use of external inputs implies a greater reliance on self-regulating processes (van Eekeren et al., 2010). Thus, organic farming systems strongly rely on soil functioning, in which soil ecosystem engineers have a crucial role. However, in a recent review, Tuck et al. (2014) highlight that the effect of organic farming on soil organisms is still ambiguous and, in general, poorly studied, especially in the South American region.

Thus, the aim of this study was to investigate if different agricultural management practices produce a replacement of earthworms by enchytraeids and the effect of that replacement on soil properties benefited by ecosystem engineering. We hypothesized that (i) tillage will change Oligochaeta community from earthworm to enchytraeid dominated; (ii) enchytraeids will replace earthworms' engineering activity, maintaining soil structure and nutrient cycling; and (iii) organic farming will favor biological-based soil functioning.

## MATERIALS AND METHODS

### Experimental Sites

The experiment was conducted in the south of Córdoba province, Argentina (33°17′ and 32°21′ S; 63°54′ and 63°46′ W). Soil

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**TABLE 1.** Farming Practices Conducted in the Agricultural Fields

| | | Crops in the Previous 7 Years | Tillage Tools | Fertilizers | Agrochemical Use | Weed Control |
|---|---|---|---|---|---|---|
| ORG | Site 1 | O-Mz/Mz/O-Sf/Sg/O-Sy/Mz/O-Mz | Disk plough (1 time), chisel plough (1 time), roll (2 times), weeder (2 times) | — | — | Mechanical |
| | Site 2 | O-Sf/O-Sg/Mz/Sf/Sy/Sf/Sy | Disk plough (1 time), chisel plough (1 time), roll (2 times), weeder (2 times) | — | *Bacillus thuringiensis* | Mechanical |
| NT | Site 1 | Sy/Sy/W-Sy/Mz/Sy/Mz/Sy | — | Sulfur | Glyphosate (7 L/ha), atrazine (2 L/ha), acetochlor (1.5 L/ha), nicosulfuron (0.5 L/ha), 2,4-D (0.4 L/ha), Chlorimuron (30 g/ha) (herbicides); chlorpyrifos (0.5 L/ha), Alphametrin (0.1 L/ha), cyclopropane carboxylate (0.1 L/ha), endosulphan (0.5 L/ha), lambdacyalothrine (0.36 L/ha)(insecticides) | Chemical |
| | Site 2 | Sy/Mz/Sy/Mz/W-Sy/Mz/Mz | — | Urea, ammonium nitrate | Glyphosate (3 L/ha), atrazine (2 L/ha), metolachlor (1.5 L/ha) (herbicides) | Chemical |
| PT | Site 1 | Mz/Mz/Sy/Sy/Sy/Sy/Sy | Disk plough and roll (2 times) | | Glyphosate (3 L/ha) | Mechanical and chemical |
| | Site 2 | Mz/Mz/Sy/Sy/Sy/Sy/Mz | Disk plough and roll (2 times) | | Glyphosate (3 L/ha) | Mechanical and chemical |

Mz, maize; O, oat; Sy, soybean; Sg, sorghum; Sf, sunflower; W, wheat; ORG, organic farming with plough tillage and occasional grazing; NT, conventional farming with agrochemical use and no-tillage; PT, conventional farming with agrochemical use and plough tillage.

is a Mollisol (USDA Soil Taxonomy) or Phaeozem (World Reference Base for Soil Resources), specifically, loamy, illitic, thermic Typic Haplustoll (Soil Survey Staff, 2010). The climate is subhumid temperate with a dry season in winter; mean annual rainfall is 840 mm, and mean annual temperature is 17°C.

Three different large-scale farming systems were studied: organic farming (ORG), plough tillage (PT), and no-tillage (NT). For that, six representative fields managed by farmers of the region using those systems were selected to have two replicates for each farming system. The ORG was characterized by the use of conventional tillage and by occasional grazing. The tillage tools used were disk plough, chisel plough, roll, and weeder. As a consequence of the large scale in which organic farming is applied in the studied region, several practices usually included in the theoretical framework of the organic production, such as the use of organic fertilizers, cover crops, green manures, intercropping, agroforestry, biological control, and so on, were not applied in the studied sites. Thus, in this study, the main differences between ORG and PT were that, in ORG, no synthetic agrochemicals were used and livestock is integrated into the management system when pasture (oat) is included as winter crop (Table 1). On the other hand, both PT and NT are conventional farming systems in the sense that agrochemical use is allowed and promoted; besides, no livestock integration occurred. Thus, the main difference between them is the use of tillage—disk plough and roll—in PT. Moreover, as a consequence of the nonuse of mechanical tools in weed control, in NT fields, a higher amount of herbicides was used. Current practices are presented in Table 1; these practices have been used for at least 10 years previous to the sampling dates. Every chosen field had more than 40 ha, and they were located in a maximum distance of 10 km to each other. To have a reference system, two grasslands (GR) of about 0.5 ha were also studied. The GR sites were natural sites, where no management or grazing was applied. They were characterized by a plant community that belongs to the Pampean phytogeographic province (Cabrera, 1976). It is dominated by *Stipa* species, and also species belonging to the genera *Brassica*, *Oxalis*, *Eragrostis*, *Poa*, *Panicum*, and *Rapistrum* were present. The eight sampled sites have the same Soil Series (according to Soil Taxonomy classifications) and were also selected by having similar geomorphological characteristics in terms of slope (1–3%) and elevation (230–250 m a.s.l.).

## Earthworms and Enchytraeids

In each of the eight fields, sampling was conducted twice in two consecutive autumns (April 2010 and 2011). Five soil monoliths (25 × 25 × 20 cm) were delimited, extracted, and then separated into two layers: 0 to 10 cm and 10 to 20 cm in depth (Anderson and Ingram, 1993). So, in each sampling time, 80 soil samples were collected and gently moved to the laboratory where they were carefully hand sorted to collect earthworm and large enchytraeid specimens (visible to the naked eye), which were fixed for 48 h in 4% formalin, then preserved in 70% alcohol and counted to obtain their density, expressed as the number of individuals per square meter. Clitellate earthworms were identified using James et al. (2015), Mischis (1991), and Righi (1971, 1979) taxonomic keys. The methodology is not the most commonly used for sampling the entire enchytraeid populations because it allows us to sample only adults. Therefore, the hand sorting of enchytraeids from soil samples was performed very meticulously, dedicating an average of 4 h for each monolith.

## Soil Functioning Assessment

Soil bulk density (BD), mechanical resistance (MR), and organic matter (SOM) content were measured as indicators of the

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soil structure maintenance function. As complementary data, soil water content (WC) was also measured.

Next to each monolith used for faunal extraction, undisturbed soil cores (0–10 cm and 10–20 cm) were extracted and transported to the laboratory where they were weighed to obtain humid weight and then dried weight (until constant weight, at 105°C) to calculate BD and WC. Mechanical resistance was measured in the field, next to each monolith, with a hand penetrometer until 20-cm depth (Bradford, 1986). Considering that measures were performed in soils with different WC, MR values were adjusted to the average of gravimetric hydric content (Parra, 2011) following the model of Busscher (1990) and da Silva and Kay (1997): $MR_{est} = a\ BD^d\ WC^h$ (where a, d, and h are parameters that depend on soil organic carbon and clay content). Finally, from the remaining soil after faunal extraction, a subsample was used to measure SOM content by the modified Walkley-Black method (Jackson, 1976).

Litter decomposition was used as an indicator of nutrient cycling functions by means of measuring weight loss of litter inside nylon mesh bags. Plant residues were collected in each field and air-dried at 30°C for 72 h before litterbag construction. One subsample of each residue was preserved to calculate the ash-free dry weight (AFDW) of the original residue used in each system. Five 10-mm mesh size litterbags (20 × 20 cm), each containing 20 g of dry weight plant material, were placed in each field in July 2009 (winter season) and secured with pegs on the soil surface. In February 2010 (summer season), litterbags were buried in the soil in fields subjected to tillage (ORG and PT sites) to simulate the same placement as that of crop residues. Litterbags were collected together with the first faunal and soil sampling, 9 months (April 2010) after field placement. In the laboratory, litter was oven-dried at 60°C for 48 h and weighed. Then, the preserved subsamples of each original residue and a subsample of the remaining litter in each litterbag were burned at 800°C for 1 h to determine AFDW and correct the percentage of remaining litter by deducting the presence of mineral soil. Litter decomposition was estimated as the percentage of AFDW remaining across time (Beare et al., 1992; OECD, 2006).

## Statistical Analyses

Oligochaeta abundances did not have a normal error distribution, so a generalized linear mixed model using the Poisson error distribution and log link function was performed (Ponce et al., 2011; Venables et al., 2011). Management system, soil depth, and the interaction term between them were the fixed factors. The sampling year, the field (nested within management system), and the subsamples (monoliths) were the random factors of the model. *A posteriori* tests were performed by the DGC test (Di Rienzo et al., 2002).

Soil properties were normally distributed, thus general linear mixed models were performed. Management system, soil depth, and the interaction term between them were the fixed factors. Sampling year, field (nested within management system), and subsamples (monoliths) were the random factors of each model. Error variance structure was modeled using management system and depth as grouping criteria and Var (Ident) of R's nlme library as variance function. *A posteriori* tests were performed by the DGC test (Di Rienzo et al., 2002). The percentage of AFDW in litterbags also suited normal distribution; hence, a general linear mixed model was performed. Management system was the fixed factor, whereas field and subsamples (litterbag) were the random factors of the model. Error variance structure was modeled using management system as grouping criteria and Var (Ident) of R's nlme library as variance function. *A posteriori* tests were performed by the DGC test (Di Rienzo et al., 2002).

All statistical analyses were performed using InfoStat software (Di Rienzo et al., 2012) used as an interpreter of R software.

# RESULTS

## Earthworms and Enchytraeids

A total of 373 earthworms and of 2,189 enchytraeids were collected. About 90% of the collected earthworms were nonclitellated specimens, and hence, we were unable to identify them to the species level. Adult earthworms found in GR were identified as belonging to five species named *Aporrectodea caliginosa, Aporrectodea rosea, Aporrectodea trapezoides, Belladrilus* species, and *Microscolex phosphoreus.* In the ORG system, *Belladrilus* species and *Microscolex phosphoreus* were found. In NT and PT, only *Microscolex phosphoreus* was present in the adult pool. All the species recorded were classified as endogeic earthworms both by available bibliography and/or by the exomorphological characterization (Lavelle and Spain, 2003; Herrera and de Mischis, 2007). Earthworm and enchytraeid abundances were significantly affected by the interaction between depth and

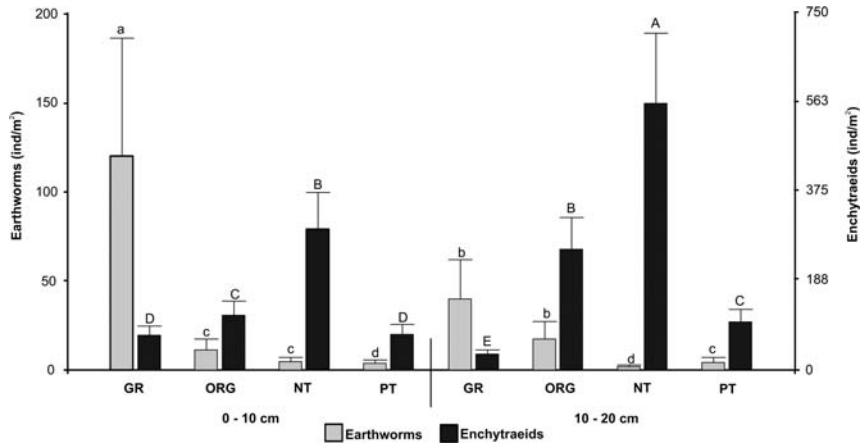


**FIG. 1.** Earthworm and enchytraeid abundances (ind/m$^2$). GR, natural grassland; ORG, organic farming with plough tillage and occasional grazing; PT, conventional farming with agrochemical use and plough tillage; NT, conventional farming with agrochemical use and no-tillage. Different letters show significant differences between systems ($P < 0.05$), lowercase letters for earthworms and uppercase letters for enchytraeids.


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**TABLE 2.** Soil Structure Indicators

| | | Bulk Density, g/cm$^3$ | | | Mechanical Resistance, MPa | | | Soil Organic Matter, % | | | Water Content, % | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Depth** | **System** | **Mean** | **SD** | | **Mean** | **SD** | | **Mean** | **SD** | | **Mean** | **SD** | |
| 0–10 cm | GR | 1.13 | 0.19 | C | 5.46 | 1.33 | B | 4.09 | 1.55 | A | 14.34 | 6.45 | A |
| | ORG | 1.10 | 0.11 | C | 1.69 | 1.05 | C | 3.03 | 0.78 | B | 11.41 | 9.31 | B |
| | NT | 1.25 | 0.12 | B | 4.34 | 2.11 | B | 2.38 | 0.55 | C | 15.94 | 7.16 | A |
| | PT | 1.16 | 0.10 | C | 2.00 | 1.34 | C | 1.97 | 1.12 | C | 12.62 | 10.17 | B |
| 10–20 cm | GR | 1.22 | 0.07 | B | 5.75 | 2.22 | B | 1.74 | 0.64 | C | 10.97 | 5.99 | B |
| | ORG | 1.22 | 0.13 | B | 5.52 | 1.80 | B | 2.15 | 0.71 | C | 10.26 | 7.98 | B |
| | NT | 1.34 | 0.08 | A | 6.80 | 2.10 | A | 2.46 | 1.00 | C | 14.56 | 5.27 | A |
| | PT | 1.35 | 0.05 | A | 6.96 | 2.08 | A | 2.26 | 0.80 | C | 12.92 | 6.86 | B |

Different letters show significant differences between systems ($P < 0.05$).

GR, natural grassland; ORG, organic farming with plough tillage and occasional grazing; PT, conventional farming with agrochemical use and plough tillage; NT, conventional farming with agrochemical use and no-tillage; SD, standard deviation.

management (Fig. 1). Earthworm abundance was greater in GR. Among agricultural systems, the highest earthworm abundance was found in ORG in 10- to 20-cm soil depth and the lowest was found in NT (10- to 20-cm soil depth) and PT (0- to 10-cm soil depth). The highest enchytraeid abundance was found in NT, and the lowest in GR both in the 10- and 20-cm soil depth. The PT was the agricultural system with lower enchytraeid abundances, whereas ORG had intermediate ones.

As hypothesized, earthworm and enchytraeid abundances had a negative relationship according to Pearson correlation analysis; higher in 10 to 20 cm ($r = -0.64$, $P < 0.0001$, $n = 80$) than in 0 to 10 cm ($r = -0.43$, $P < 0.0001$, $n = 80$). Moreover, their mutual exclusion did not have the same pattern in the different management systems. To analyze this, the mean number of enchytraeids on per-earthworm basis was calculated (Enchytraeidae-to-earthworm ratio). Indeed, although the net enchytraeids abundance was higher in ORG than in PT, 10 less enchytraeids for each earthworm were found in ORG than in PT (Enchytraeidae-to-earthworm ratio of 12.4 and 22.1, respectively). At opposite extremes, GR had less than one enchytraeid for each earthworm and, on the other hand, NT had 189 enchytraeids for each earthworm.

## Soil Functioning

Soil property results are shown in Table 2. Soil compaction was highest in NT and PT in 10- to 20-cm soil depth according both to BD and MR. The lowest compacted soils were found at first depth of GR, ORG, and PT. The highest SOM content was observed in 0- to 10-cm soil depth of GR. Among agricultural systems, the soil belonging to ORG farming in 0- to 10-cm depth had the highest SOM content. In all the other cases, no differences in SOM were observed. The GR and NT were the systems that better conserved the water content in 0- to 10-cm soil depth. In the 10- to 20-cm depth, NT had a higher WC than all the other systems.

The ORG had the highest litter decomposition rate (Table 3), an intermediate decomposition rate was observed in PT, and the lowest rate was found in NT. Unexpectedly, GR was the system with the lowest litter decomposition rate.

## Earthworms, Enchytraeids, and Soil Functioning

According to Pearson correlation analyses, earthworms were strongly associated with high SOM contents ($r = 0.74$, $P < 0.0001$, $n = 160$) and low BD values ($r = -0.43$, $P < 0.0001$, $n = 160$), that is, GR and ORG soils. On the other hand, the low earthworm abundances found in NT and PT can be explained by the low soil physical quality according to those parameters. Enchytraeids were related to more compacted (BD and MR, $r = 0.54$ and 0.35, $P = 0.00$ and $P < 0.0001$, $n = 160$) but humid soils ($r = 0.43$, $P < 0.0001$, $n = 160$), showing their highest abundances in NT soils.

A positive relationship was found, in the agricultural systems, between earthworm abundances and litter decomposition ($r = 0.58$, $P = 0.00083$) (assessed in the first sampling date, when decomposition was measured). However, in GR, the highest earthworm abundances corresponded with the lowest decomposition rate. No significant relationship was observed between enchytraeids and decomposition.

# DISCUSSION

## Earthworms and Enchytraeids

Earthworms and enchytraeids have been reported as having different responses to agricultural practices. Specifically, tillage has been proposed as the driver that causes shifts from earthworm- to enchytraeid-dominated soils (e.g., House and Parmelee, 1985; van Vliet et al., 2004; Wickings and Grandy, 2013). Furthermore, no-tillage practice has been associated with more abundant and diverse earthworm communities (Kladivko, 2001; Brown et al., 2003). This shift has been related to the combined effect of a greater competitive ability of earthworms in undisturbed and suitable conditions for their survival and by a greater ability of enchytraeids to survive in highly disturbed soils (Cochran et al.,

**TABLE 3.** Remaining Percentage of Ash-Free Dry Weight Obtained From the Litter Decomposition Experiment Conducted in Each System

| System | Mean, % | SD | |
|---|---|---|---|
| GR | 39.88 | 2.43 | A |
| ORG | 5.84 | 1.62 | C |
| NT | 39.33 | 3.49 | A |
| PT | 13.53 | 1.76 | B |

Different letters show significant differences between systems ($P < 0.05$).

GR, natural grassland; ORG, organic farming with plough tillage and occasional grazing; PT, conventional farming with agrochemical use and plough tillage; NT, conventional farming with agrochemical use and no-tillage; SD, standard deviation.

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1994; Wardle, 1995; Nowak, 2004). The negative relationship between the two Oligochaeta groups was corroborated in our study, but tillage was not the main factor involved. Earthworms were not favored by no-tillage, having very low abundances in both conventional management systems, with and without ploughing. Furthermore, among agricultural systems, ORG had the greatest earthworm abundances despite the high-intensity tillage performed. Negative effects of glyphosate and chlorpyrifos, the former used in both conventional managements and the latter in NT, on earthworm reproductive and activity patterns have been previously reported (e.g., Paldy et al., 1988; Springett and Gray, 1992; Cox, 2000; Casabé et al., 2007; Santadino et al., 2014). Hence, agrochemical use could be a leading factor involved in diminution of earthworm abundance in farming soils. Similar results were found by other authors when comparing plough tillage in organic and conventional farming (Siegrist et al., 1998; Bettiol et al., 2002; Suthar, 2009). However, it should be noticed that earthworm abundance suffered an important diminution even in ORG with regard to natural grasslands. Although earthworm richness was evaluated only in the adult pool and thus probably underestimated, it also decreased in agricultural systems from five to two species and one species in ORG and conventional farming, respectively, with regard to GR. This result agrees with Duhour et al. (2009) who also found a decrease from nine to three species in GR and cropped sites, respectively, in similar systems to those studied here. Moreover, Brown et al. (2004) also found a decrease in earthworm richness when comparing some native with introduced pastures. Earthworm's richness decrease in agricultural systems is likely related to high physical disturbance on agricultural soils, especially in tillage systems. In addition to this, the decrease in all the agricultural systems of vegetal richness and diversity is related to a decrease in spatial heterogeneity and in diversity and availability of organic matter resources. Thus, only species highly resistant to those changes and conditions remain present on agricultural systems.

Enchytraeids had the greatest abundance in NT fields; NT fields also had the higher Enchytraeidae-to-earthworm ratio, with 189 enchytraeids for each earthworm. These results do not agree with several previous findings in which enchytraeids have been enhanced by tillage (House and Parmelee, 1985; Kladivko, 2001; Wickings and Grandy, 2013). It has been suggested that, in tilled soils, the positive effects of having more available food in the soil profile counteract the negative effects of mechanical tillage (Cochran, et al., 1994). However, other studies have found a positive effect of reduced or no-tillage on enchytraeids. For example, Parmelee et al. (1990) found enchytraeids consistently more abundant in no-till than in conventionally tilled plots in Typic Rhodudult soils in subtropical climate. In the same region, the same trend was also observed by van Vliet et al. (1995). In our study, detrimental effects of mechanical tillage appear not counteracted by the increase in the availability of organic resources. Nonetheless, enchytraeids were more abundant in ORG than in PT despite higher earthworm abundances and similar tillage regimes. A higher residue input and diversity, because of both higher crop diversity and higher weeds biomass, and the nonuse of agrochemicals could explain the positive effect of ORG on enchytraeids in comparison with PT. However, higher enchytraeid abundance was found in NT regarding PT despite the higher amount and variety of agrochemicals used in NT. Therefore, this would not explain the differences. Higher enchytraeid abundance in NT is more likely explained by the absence of competition by food resources because of the very low earthworm abundance found in NT, confirming the negative relation between enchytraeids and earthworms.

With regard to depth distribution, previous studies have suggested that, in NT system, enchytraeids are more abundant in the top 5 cm of the soil, whereas tillage causes a more even distribution over the soil profile (van Vliet et al., 1993, 1997). However, in our study, the highest abundances in crop systems were found at 10- to 20-cm depth regardless of the tillage system.

## Soil Ecosystem Engineering

Soil properties assessed in this study are involved in reciprocal relationships with earthworms and enchytraeids, affecting and being affected by them. So the observed exclusion between these two groups can be partly explained by differences in such properties and *vice versa*: their differences in performing ecosystem engineering activities can partly explain the differences in the soil properties.

Soil structure deterioration has been frequently observed in agricultural soils (Topoliantz et al., 2000), and earthworms and enchytraeids have a lot to contribute in solving this issue. Hence, in this study, BD and MR were assessed as indicators of soil structure maintenance. Our results show that tillage by itself was not enough to avoid compaction in the whole depth, as intermediate compacted PT soils demonstrated. However, tilled soils with higher earthworm and enchytraeid abundance (ORG sites) had values of soil structure indicators similar to those found in GR soils. This emphasizes the likely relevance of earthworms in maintaining soil structure through the formation of both biopores and aggregates, resulting from their feeding and burrowing behavior (Lavelle and Spain, 2003), even in tilled plots. Indeed, high earthworm abundance, as well as the presumably high abundance of the rest of soil biota and the higher vegetation diversity typical of GR, was very likely related to the low BD found in those soils.

It has been suggested that enchytraeids, through their feeding activity, cause a fine-grained crumb structure in the soil with stability often higher than that of bulk soil (Jänsch et al., 2005). Furthermore, their burrowing ability may improve the fine-scale water and air management of the soil (Jänsch et al., 2005). However, our results show that enchytraeids were not able to counteract soil compaction produced by NT despite their very high abundance, rejecting our hypothesis that enchytraeids can replace earthworm engineering activity. Enchytraeid influence on soil structure was recorded by several researchers. Didden (1990) found higher air permeability, volume of pores, and proportion of aggregates when enchytraeids were present (five cocoons in 55 g of soil). Van Vliet et al. (1993) also observed an increase in soil porosity in a microcosm study because of enchytraeid activity (measured with 20 enchytraeids in 90 g of soil). However, at a later time, they also observed an increase in the soil consolidation and hypothesized that enchytraeids refilled the pores with excrements and decreased the aggregate stability by passage of the soil through their guts. Our results in NT systems may be partially explained by a mechanism similar to this. Furthermore, soil compaction itself may be a detrimental factor on enchytraeid abundance (Langmaack et al., 1999; Beylich et al., 2010). In our study, the levels of soil compaction found are suggested as not high enough to inhibit soil colonization by enchytraeids. However, we suggest that physical conditions could have limited their microengineering activities, which would have been a key factor in avoiding soil structure deterioration in NT soils.

The maintenance of soil structure is a largely complementary process to the decomposition of organic residues. Organic matter has important effects on soil structure both in colloidal form and as larger particles, and the energy released through the decomposition process is used by organisms for bioturbation, an important process in the creation and maintenance of soil structure, and in soil formation (Lavelle and Spain, 2003). Hence, SOM content is a major driver of several soil ecosystem processes, and the


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process of litter decomposition has been recognized as a key function in agroecosystems (van Vliet et al., 2004).

In our study, SOM was higher in the grasslands in 0- to 10-cm soil depth, as expected. Furthermore, SOM was considerably benefited in organic farming soils with regard to both conventional systems. This result agrees with García-Ruiz et al. (2009) and Mazzoncini et al. (2010) who also found higher SOM contents in organic than in conventional agriculture. Considering that organic fertilizers or amendments were not used in ORG, we explain the high OM content mainly by a more active soil biota and by a higher carbon input related to the inclusion of pastures in the rotation cycle. On the other hand, we found that both conventional systems—NT and PT—had similar SOM values, which question the rather established concept that NT conserves and even increases SOM content with regard to tilled systems (Díaz-Zorita et al., 2002; Thomas et al., 2007; Ernst and Siri-Prieto, 2009; So et al., 2009). This can be related to a similar crop residue input even though, in PT, crop residues are buried whereas, in NT, crop residues remained in the soil surface.

Earthworm abundance was highly and positively related to SOM content, which agrees with the widely recognized relevance of SOM on the development and maintenance of earthworm communities (Edwards and Bohlen, 1996; Ayuke et al., 2011). This result also highlights the importance of achieving the maintenance and/or increase of SOM in agricultural soils. Although benefits of organic matter on enchytraeids have been suggested (Jänsch et al., 2005), we found no correlations of their abundance with SOM content.

Indirect evidence about soil functioning with regard to nutrient cycling and soil structure is provided by the SOM content itself but in field evaluation of litter decomposition is also a very valuable indicator. Although microorganisms are responsible for the biochemical degradation of organic litter, soil fauna is important in the decomposition of litter through the facilitation of microbial actions. Earthworms break up the plant material; expose organic surface areas for microorganisms' action; move fragments and bacteria-rich excrement around, up, and down; and function as homogenizers of soil strata (Coleman et al., 2004). In a smaller spatial scale, the same actions are performed by enchytraeids (Cole et al., 2000; van Vliet et al., 2004).

Litter decomposition was significantly higher in ORG than in PT and in both higher than in NT. The highest decomposition in ORG agrees with Fließbach et al. (2000) findings where percentages of respired C in soils from organic agriculture were higher than from conventional agriculture. Besides, they suggest that farming practices in organic agriculture promote a higher efficiency of the microbial community in substrate use for its growth. Moreover, the highest decomposition in both systems with tillage is explained because buried litter maintains a higher water content and supports greater densities of all microflora and fauna than surface litter (Beare et al., 1992). Indeed, in both conventional systems (PT and NT) where the same residue (soybean) was used in the litterbags, decomposition rates were higher in PT. On the other hand, as residues in ORG and PT were not the same, a similar decomposition rate could be expected considering litter placement; or a minor decomposition rate in ORG as litter quality according to C:N ratio of residues used in ORG was lower than soybean quality (McKinney et al., 2004; Babu et al., 2014). However, although residue placement was the same in ORG and PT systems, litter decomposition was significantly higher in the former; thus, the relevance of earthworm activity arises, suggesting a positive influence of earthworms on decomposition in agricultural soils. Although we expected that the high enchytraeid abundance found in NT could contribute to litter decomposition and compensate the lack of earthworms, very low decomposition values were observed. We hypothesize that this fact is explained first by the litter placement in NT, which causes unsuitable conditions for the soil biota to access the residue (Beare et al., 1992); second, by the very low earthworm abundance in NT, which do not incorporate residues into the soil profile; and third because it is likely that soil compaction can decrease the ability of enchytraeids to enhance decomposition (Roithmeier and Pieper, 2009).

The low decomposition rates observed in GR was an unexpected result, but it would be explained because of several factors. First, the original residue from GR sites is less palatable for soil biota than residues from agricultural sites because natural vegetation in GR has much higher lignin content and a lower C:N ratio (Saparrat et al., 1998; Johnson et al., 2007). Second, GR are systems with a long-term natural equilibrium between the humification and mineralization processes, where plant community nutrient consumption is also in equilibrium with nutrient release from litter (Haynes, 2005; Horwath, 2007; Marinari et al., 2007). Annual fresh litter input to the soil is higher than in cultivated systems, and therefore, the nutrient release equilibrium is achieved with lower decomposition rates. Soil organic C in natural temperate GR is expected to increase because the annual input of C to humic substances exceeds mineralization, and this positive C balance results in an accumulation of C in soil (Buyanovsky et al., 1997; Collins et al., 1997). And finally, the addition of litterbags in GR may not represent a necessary resource for soil biota, unlike in agricultural systems where litterbags may constitute a hot spot of organic resources. Even so, the decomposition rate in GR was similar or even higher than that found by Koukoura et al. (2003) and Moretto and Distel (2003) in temperate GR.

## CONCLUSIONS

In agroecosystems, natural and biologically mediated processes like those regulating soil structure, nutrient supply, and pest and disease control have been largely replaced by human inputs (i.e., soil tillage, fertilizer and pesticide applications) that ultimately depend on nonrenewable energy sources (Barrios, 2007). To attempt for a more sustainable agriculture, external inputs are intended to be highly reduced, which implies a greater reliance on self-regulating processes like ecosystem engineering (Brussaard et al., 2007).

Soil biota and specially soil ecosystem engineers have an outstanding relevance in farming systems that are intended to be sustainable either in organic farming or in no-till, which are considered as the more sustainable farming systems. In our study, we confirmed the idea of mutual exclusion between earthworms and enchytraeids. However, the change of the dominance of earthworms to enchytraeids was not directly related to tillage intensity, and therefore we reject in part our first hypothesis. That change was instead mainly related to the negative effect of agrochemicals on earthworms, which likely caused their lower abundances that were in turn related to higher enchytraeids' abundance, suggesting a high relative importance of competitive interactions. We reject our second hypothesis regarding enchytraeid ability to replace earthworm engineering. The very high enchytraeid abundance found in no-tillage was not able to favor soil structure and nutrient cycling indicators. The high soil compaction caused by continuum no-tillage of the soil may be restricting biotic activity, which, even when abundant, cannot outweigh the compaction process. We confirmed our third hypothesis because organic farming promoted intermediate abundances of earthworms and enchytraeids, which maintained a soil structure similar to GR and enhanced nutrient cycling process.

It is worth highlighting the importance of ecosystem engineer community in improving soil functioning. Organic farming was

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the best system for accomplishing this with an active soil fauna community, although recommended practices such as cover crops, green manure, intercropping, biological control, and so on were not applied in the large-scale farms studied.

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